

BIOLOGICAL BULLETIN

NOTES ON THE BEHAVIOR OF THE FIDDLER CRAB.

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There exists already a small literature dealing with habits of fiddler crabs and the general biology of these forms is known fairly well. As far as I am aware none of the various reactions of the animals, however, has yet been studied thoroughly. A *careful* study of the movements of an animal undoubtedly differs from a general one not merely in bringing some new details, but as well in bringing quite new problems. I quote Schwartz and Safir: "Correlated with the regular recurring changes in the tide, *Uca* performs its tasks with unchanging regularity, its general behavior never deviating from its standard, never altering from its established method, being almost stereotyped" (18 p. 20). "It has few tasks to accomplish, and does them day in and day out in the same way" (*ibid.*). From a certain point of view a crab has but a few tasks to accomplish, as digging the burrow, feeding, fighting and performing its sexual activities. From a similar point of view the "general behavior" of man is also a monotony of reactions, like dressing, undressing, eating, walking, talking and sleeping. However we do not consider the man as being a stereotyped automate because we know a lot about our own life, and we know that every one of those reactions may be performed in infinitely different ways. And yet a careful observation of the activities of a fiddler crab leads to very similar conclusions. Every individual digs its burrow but the details of this process may be infinitely various and the behavior of the animal is as far as possible from a stereotype.

My time being very limited I succeeded in observing but few

particulars. Nevertheless they seem to indicate that the existing literature on the fiddler crabs has not exhausted all possibilities.

THE BURROWING INSTINCT.

All my observations were done on *Uca pugilator*, the sand-fiddler. In the environs of Woods Hole this species lives on sand banks communicating with the ocean by means of a complicated system of ponds and channels. On account of this circumstance the rising tide is very quiet and the animals are never exposed to waves. In fact so slow is the movement of the water that at the low tide one may see clearly sand-pellets removed by the animal from its burrow during the previous low tide. This particular is rather important to note, as many habits of *Uca* are correlated even with slow tidal changes.

Watching the animals in the field furnishes only data which are already known and there is no need to relate them once more. But one particular concerning the shape of the natural burrows deserves some attention. I studied it, pouring a solution of white plaster into the burrow and digging the mould out after it became hard. According to Pearse (12, 13) the burrows of *Uca pugilator* rarely exceed 75 cm., which I found to be correct. The burrows are nearly always oblique to the surface of the ground and they show a general tendency to become somewhat horizontal at the inner end. But there are very many modifications and it would be rather difficult to say which is the type. Sometimes the beginning of the burrow is vertical and then it bends sharply, as in Fig. 1, *a*; sometimes the inner end of an oblique burrow suddenly becomes vertical as in Fig. 1, *c*. They show, however, some common features, as they are always somewhat bent, never perfectly straight. Every burrow ends with a marked swelling—the end-chamber—where the animal often remains. In some cases the end-chamber is so large that its inhabitant may turn in it in every direction, in others it allows only turning around the transversal axis of the body. I failed to notice any difference connected with the sex of the crab. Also I have never seen a branching passage, as described by Cowles for *Ocypoda arenaria* (5). I found such a passage in some burrows of *Uca pugnax* but the burrow of *Uca pugilator* is

always a simple tube. It is difficult to say to what conditions may be due the marked individual differences in the shape of the burrows, as the external conditions on a horizontal bank of pure sand seem to be perfectly uniform for all individuals. Referring them to the different individuality of the crabs may be true, but probably it means nothing more than our complete ignorance of the causes.

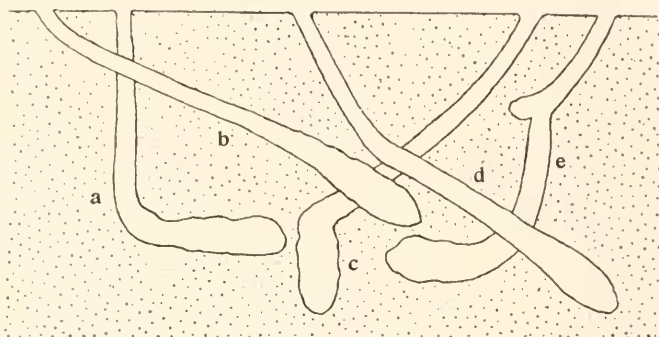


FIG. 1. Different types of natural burrows.

To be able to watch closely the process of burrowing we must observe it in the laboratory. In cylindric glass-jars (6 inches in diameter, 9 inches high) half filled with wet sand the crabs struggle madly and try to escape by climbing on the glass wall, in which they are of course unsuccessful. The animals remain near the wall and particularly near the most lighted spot of it. After some time the movements become slower, the crab gives up its attempts to escape and it keeps quiet for a while in its normal position. Finally it begins to dig. The individual behavior may be very different. Some crabs start their work after a few minutes, others roam around the jar for hours and even days. Some remain motionless for many hours, others move perpetually and struggle for escape. Some may walk around the wall showing no particular predilection for the lighted side, some again remain for a long time at the spot nearest to the window. There is a slight difference between the sexes, the females being more shy on the average and starting the work sooner. The mode of working is also somewhat different in both sexes, which will be mentioned later.

We come to our first question: on what conditions depends the spot at which the animal starts digging? The spot is not quite a random one as some rules seem to hold. Practically in all cases the hole lies close to the wall of the jar and at least very often the wall directed towards the light is preferred. The answer is a simple one. The crab is both positively phototactic and thigmotactic. During its struggling for escape *Uca* remains at the most lighted spot of the wall; there it quiets down and there it begins to dig. This explanation may be correct, but it leads to further considerations. Phototaxis means of course an overwhelming reaction towards the light, and only in this sense it has a definite meaning. We are also positively phototactic and we do not like to remain in the dark. Nevertheless nobody would explain the reactions of man on this basis as our phototaxis is checked by very many other reactions. Such an explanation, however true in some cases, would be one-sided and rather poor. But the same holds also for the crab. The animal is positively phototactic, and yet it digs a burrow which conducts it away from the light. During the burrowing *Uca* repeatedly comes out of the hole towards the light and it enters the burrow which is dark. Is then the phototaxis changing with every minute? In the jar the crab keeps usually close to the wall during the whole work and the whole burrow may be fully exposed to light, which does not disturb the animal in any way. After having finished the work and after having filled the burrow almost entirely with sand, as described below, the crab remains at the bottom of the jar, in the end-chamber, which is often fully lighted, and it may remain there motionless for days. We can compel the fiddler to dig in the middle of the jar making there a shallow hole and driving the crab into it. But as the burrow is oblique the animal soon reaches the wall of the jar at some particular spot and it makes an end-chamber there, being by no means disturbed by the light. We must consider that a similar situation never occurs under normal life conditions of *Uca* as the hole always leads to the dark. The natural burrows have their openings just as often directed to the south as to the north. All the evidences indicate very strongly that under fairly normal conditions of life *Uca* is insensible to light, or, to say it more correctly,

phototaxis does not play any marked rôle in its life. According to Schwartz and Safir on cloudy days the fiddlers remain inactive. On the contrary, in my laboratory hundreds of fiddlers displayed the most activity in the dark which may depend on being undisturbed when nobody remained in the room. The inactivity on cloudy days is surely connected with heat, not with the light. What we call phototaxis in *Uca* may be observed only under very unnatural conditions when the crab is struggling blindly for escape. Its activities are then uncontrolled by the inhibitory centers and automatic correlations may drive the animal towards the light. Such cases are very interesting for a study of automatic nervous connections but they are scarcely valuable for psychology.

As to the thigmotaxis some observations point to its existence. In the dark *Uca* also dig their holes near the wall but of course no particular spot of it is preferred to the others. And again a control experiment shows that the thing is not so simple. I put several crabs into a large crystalliser (11 inches in diameter) filled with sand. I thrust in the sand several small glass plates at different spots, covered the crystalliser and put the whole in the dark. If remaining close to the wall be only a matter of thigmotaxis we might expect that the crabs will dig just as often near the glass plates scattered through the whole surface of the sand, as they dig near the outer wall. But in fact from 26 crabs tested several times only one made the burrow near a peripheral glass plate, all others dug invariably close to the outer wall. And yet the sum of contact surfaces of all plates with the sand was even superior to the surface of the crystallizer's wall. Once more the thigmotaxis proves to be not an adequate explanation. The tendency of the crab is not to remain by the wall but to remain at the very periphery of the vessel. Under similar conditions practically all animals show the same behavior, *Paramœcium* as well as man. As I showed (6) *Paramœcium* swims along the periphery of the vessel in spite of its thigmotaxis being negative while swimming. In a closed place which we wish to leave we will be oftener found at the periphery than in the middle of it. The reaction has nothing to do with thigmotaxis.

Besides photo- and thigmotaxis there is a strong hydrotaxis, the crab striving towards the moisture. There exists also a very marked tendency of hiding itself in the sand. Especially in females we may see often a behavior distinctly different from the ordinary burrowing. It consists in a quick pressing of the body in the sand. As the friction is very strong the animal succeeds only in hiding the thorax while the legs of one side of the body remain uncovered. In this position the crab may remain motionless for hours and such a behavior certainly has some biological significance as very little is seen of the crab, the legs having a marked protective coloration. The consistency of the ground has also some influence on the choice of the spot where the work is started. If we make a shallow hole in the sand *Uca* will choose it as the starting point. All those "taxies" and strivings, and many more, determine the actual behavior and referring the activities of a crab to some particular tropism is rather a poor explanation.

However, at last the animal starts its work. To simplify the nomenclature I shall use roman numbers I.-V. for the legs of the side of the large claw of the male, and the arabic 1-5 for the legs of the opposite side. Thus I. means the large chela, 1 — the small one.

At the very beginning of the work the side 1-5 is usually directed towards the wall of the jar, straightly or obliquely, and usually this side begins to dig. The legs 2, 3 and 4 which are

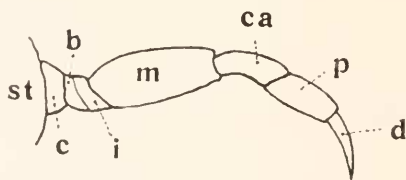


FIG. 2. The second leg from the side. *st*, sternum; *c*, coxopodite; *b*, basipodite; *i*, ischiopodite; *m*, meropodite; *ca*, carpopodite; *p*, propodite; *d*, dactylopodite. There is no movable articulation between *b* and *i*. Articulations *p-d*, *m-ca* and *c-b* work in the same plane, others at right angles to them.

bent in the articulations mero-carpopodite and dactylo-propodite at the normal position of the body become somewhat stiff. At the next moment they become bent a little more in both articu-

lations mentioned above and the terminal hooks (dactylopodits) sink into the sand. The legs are not bent at once but one after another in a quick rhythm which helps to make the sand lighter. If the sand is hard those efforts are repeated, until the whole dactylopodits and a good part of propodits enter into it. A portion of sand lies now between the legs 2, 3, 4 and the side of the thorax. Now the legs become also bent in the articulation coxo-basipodit which works in the same direction as the former two. The portion of sand becomes loosened from the ground and tightly pressed to the side of the carapace. The crab walks a few centimeters aside carrying the sand, then it stops and the legs 2, 3, 4 become bent also in the articulation sternum-coxopodit working nearly at right angles to the former three. Through this movement the pellet is directed towards the sagittal plane of the body and forward. It is pushed in this direction by the side surface of the working legs. A further bending of the same articulation causes the legs to touch the pellet with their external surface. As soon as this occurred the legs become extended in the articulation mero-carpopodit one after another as at the beginning. The pellet may be now pushed still further towards the side I.-V. The sand is not very wet at the surface and the pellet does not hold together. The loose sand grains are to be prevented from falling back into the hollow remaining at the place of the removed pellet and the crab does it very carefully. In this work of pushing away the sand which is not any more held by the legs the small chela helps also. Very often it starts helping even before, when the pellet is first formed, pushing it together with legs 2, 3, 4. But it is never used for digging in the proper sense. The leg 5 also remains inactive in digging as it has a different task to accomplish. After having pushed the sand away, removed the grains that remained on the legs and kneaded the sand a little the animal returns to the hollow and grasps another portion of sand in the same way. But even the second pellet brings some difficulty with it as it is never carried far away and the loose grains of sand easily roll back. Therefore as the work progresses, more and more legs participate in it. Besides the legs 1, 2, 3, 4 the leg II. begins to help. When the pellet is already pushed beyond the sagittal plane of the body

the leg II. strongly bent in the articulation mero-carpopodit comes behind the pellet touching it with the external surface of pro- and dactylopodit. Extending the leg II. in the mentioned articulation the crab pushes and kneads the sand in the same way as do the legs 1-4. A little later also the legs III. and IV. are used in the same manner. Then the large chela begins to play its part. Its lower edge is held closely to the surface of the ground and extending the leg in the articulation mero-carpopodit *Uca* pushes from time to time large portions of sand away as with a spade. Many authors (Alcock, Pearse) consider the large claw of *Uca* as being a secondary sexual character. But it plays also an important rôle in digging.

The deeper the burrow becomes the higher is the sand hill at its mouth and the greater is the danger that the sand will roll back. All legs, excepting V. and 5, participate in pushing it away and this work is done more and more carefully. At the same time the sand from the deeper layers is more wet and the grains hold together better which facilitates the task. The pellets may be simply rolled away from the mouth of the burrow. In this action again all legs participate and the digging side presents the pellet to the pushing side which rolls it farther. The legs II., III., IV. push the pellet with the external side of their pro- and dactylopodits, the crab walking after it sometimes at a considerable distance. In the field the removed pellets often lie as far as one meter from the mouth of the hole. Sometimes when the chela I. has pushed a pellet far away it will do the same with some other pellets before the animal returns in the hole, as if the crab wanted to mend its former inaccurate work. The more sand is carried out the farther the crab rolls the pellet; sometimes it is deposited at the opposite side of the jar. The large chela, as mentioned, is used only from time to time; it does a rough work. In most cases it would only disturb the rolling of the pellets. Therefore it is always raised high in the air in the moment when the side 1-4 presents the pellet to the side II.-IV.

There is still the problem of locomotion to be solved. As known, during the sidewalk of crabs the legs directed forward pull the body while the opposite legs push it. As the digging

work progresses the crab has to carry its burden from a greater and greater depth. The legs II.-V. are free in pulling the body, but the legs 2-4 are holding the sand. The chief rôle in the locomotion on the inner side is played by the leg 5 which is never used for burrowing. In the later stages of burrowing the leg 2 also begins to help a little. Its articulations pro-dactylo-podit and mero-carpopodit are moving and pushing the body, while the meropodit holds the pellet. To a certain extent also the small chela helps. Only the legs 3 and 4 remain motionless, holding the sand.

Another interesting particular. When the burrow is just deep enough to hide the thorax but the legs I.-V. remain outside, the crab often grasps the edge of the hole with legs II.-V. helping to move the body out of the burrow. There is the danger that the edge will break under this effort and the sand will fall into the burrow. Thus the crab grasps the edge at four points possibly distant from one another embracing about 160° of its circumference. In all other cases the legs are held much closer together.

The burrow is perfectly circular in every transverse section. This becomes possible because the crab changes very often its position within the tube turning around the transversal axis of the body. As the canal of the burrow is oblique the animal sometimes walks along it having its legs directed towards the upper wall and the back touching the lower one. Consequently *Uca* comes out from the burrow touching different points of the hole and this causes the pellets to be deposited at different spots around it. But the most of them are deposited in the direction which is a prolongation of the inclined burrow. Evidently walking along the lower wall of the canal is easier and occurs oftener.

Still repeating all those described movements the animal succeeds in digging a deep burrow ending blindly at the bottom of the jar. However sometimes *Uca* stops digging before the bottom is reached. As mentioned above the inner end of the burrow forms a kind of chamber markedly larger in diameter as compared with the canal. The animal is especially careful in making it and often it will spend hours in finishing the end-

chamber. The principal instrument is now the small claw which is repeatedly pressed with its external surface against the wall flattening the sand and hardening it. During the work the crab changes its position and it is often to be seen lying on its back and working at the roof. When the burrow is finished the animal will remain motionless, sitting in the end-chamber for a long time.

The female works in a closely similar way. But as both chelæ are equal there is no preference to either side of the body. In pushing the sand the claw of the side external to the burrow works as the other legs. From time to time the female will change the working side. On the average the work is accomplished a little sooner than in the male which is possibly due to the changing of the side digging which gives to it a chance for resting. One observation points in fact that the legs may soon become tired. When a crab runs along the sand for some paces it will stop from time to time quickly changing the side directed forward.

If the crab meets any obstacle while digging, its behavior depends very much on the stage of the work at which this occurred. Small stones are simply carried out like a sand pellet. Bigger stones which are too heavy for the animal cause an abandoning of the hole if they lay near the surface. In such cases the animal will start digging another burrow at some spot near to the first, changing the spot many times until it finds a suitable one. But if the obstacle lies deeper the efforts of the crab may last for a long time and often it rather prefers to change the direction of the burrow than to abandon a work which is half done. This has been observed already by Schwartz and Safir. The peculiar form of the burrow on the Fig. 1, *e*, is due to changing the direction of burrowing on account of some obstacle.

The described typical mode of working is connected with many difficult problems.

1. There is the characteristic shape of the burrow to be explained. If we make a perpendicular hole in the sand about 5 cm. deep and drive the crab into it the animal soon starts working. But it never goes in the direction of the hole. The

burrow becomes bent and it approaches continually to the horizontal plane. This tendency explains to a certain extent why the burrow is never straight. The animal must hide itself in the sand and the shortest way of doing it would be the digging in a vertical direction. On the other hand the burrow must approach the horizontal line. Both tendencies working together cause the burrow to become bent. From a mechanical point of view we might expect that the crab will dig in the direction of a diagonal. Thus the burrow forming a curve shows that the causes are more numerous and a mechanical explanation is far too simple.

The biological significance of the end-chamber and of the burrow being bent follows from a simple experiment. When the animal has finished its work and it is sitting motionless in the end-chamber we begin to drop slowly sea water into the jar. Very soon the water reaches the crab. The animal begins to stir, then it climbs up to the mouth of the burrow and closes it. To do this *Uca*, usually sitting in the burrow with its large chela directed towards the entrance, goes entirely out, turns and enters the burrow with the chela I. forward. When the body is so deep that the bent legs 2-5 touch the edge of the hole they grasp this edge and pull it strongly inward. This time the legs are held close together and the leg 5 participates in the work like the others. There results a pellet of sand which is dragged down and adjusted carefully to the side wall of the canal close to its entrance. The pellet is followed by the second, third, etc., until a solid cork is formed closing tightly the hole. On the surface of the sand at the spot where the hole was, there remain radial furrows converging towards the former center of the hole. This process was already described by Pearse and others. But the task is not yet finished. *Uca* grasps the sand inside the burrow and carries it to the top, adjusting the pellet to the new formed roof of the hole. Very many pellets may be handled in the same way and a thick cork arises which closes the burrow tightly. We may pour so much water as to cover the sand completely. If at the beginning we dropped the water in very slowly the animal had enough time to close the burrow carefully. In this case, and such is the case under natural

conditions, even under the water there remains always a waste chamber where air is retained and in which the crab remains until the tide goes out. This process may become modified in several ways. Very often *Uca* adjusts the sandcork in the middle of the canal without rising to the mouth of it. The end result remains the same, as the cork is also very tight. If we pour the water a little quicker the crab works in a great hurry. It rises to the top and it simply pulls many pellets of sand down without adjusting them. Sometimes the animal has no time to turn its large claw inward and it works hastily with II.-V. legs as well as it goes. Finally, if we pour the water very quickly, the burrow remains open, water enters into it, and the walls of the canal collapse burying the animal. In such a case *Uca* usually very soon digs itself out and remains on the surface of the sand until we suck the water out with a pipette. In the field such an accident may be caused by a rain shower.

These observations pour some light on the biological significance of the burrow being bent and the end of it approaching the horizontal line. In such a burrow the end-chamber may be easier preserved from being filled with water. The air-chamber sometimes may be vertical as in the Fig. 1, *c*. But the foregoing part of the burrow is then strongly bent and the end result remains the same. Such air-chambers are known for several sand crabs, as for *Dotilla* (Symons, 19) and others.

Exactly speaking, the detecting of the biological significance of the shape of a burrow does not tell us anything about the factors that cause it. Beyond any doubt the direction of burrowing is closely connected with gravity. This follows from some experiments. In order to be able to watch closely the process of burrowing I constructed a simple apparatus. Two glass plates fitting closely into a jar in vertical position and reaching about two-thirds of its height were put into the vessel. Four corks of a suitable size (about 2 cm. thick) were put at four corners between the plates and the whole was held together with four threads. Thus the plates formed a kind of box and the 2 cm. wide space between them was filled with wet sand. Over this box standing vertically in the jar I put a round piece of cardboard fitting exactly to the jar and having a cleft in the

middle corresponding to the space between the plates. If we put a crab into the apparatus it begins to dig and as it can dig only between the plates it may be watched during the whole work. When the crab reached about the half of the height of the sand column I turned the apparatus at right angles. *Uca* changed then the direction of digging, working now nearly at right angles to the previous direction. Some of such burrows may be seen in Fig. 3.

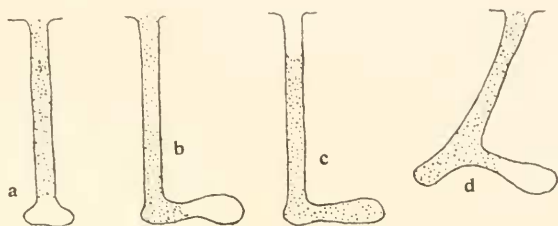


FIG. 3. Effect of turning the apparatus at 90° a, b, c, burrow of the same individual. For explanation see the text.

Clark (4) extirpated both inner antenna of *Uca pugilator*. He states that the normal equilibrium of the animal was somewhat damaged and there was a tendency to roll over. But at the same time the normal conditions, as feeding and burrowing, remained unaltered. Clark has not investigated the shape of the resulting burrows which could possibly furnish some interesting conclusions. For the moment we can say only that gravity is one of the factors affecting the shape of the burrow.

2. Another question connected with burrowing is the question of breathing. The interesting paper of Abbott dealing with the effect of distilled water upon the fiddler crabs (1) contains many important data. The gills of *Uca* are situated at the bottom of the large gill-chamber and the space over them is filled with liquid. Abbott thinks that this liquid has only about one-fifth of the concentration of the sea water. The gill-chamber communicates with the exterior by means of a canal, the opening of which lies between the basal joints of third and fourth legs. In this way the liquid of the chambers may exchange gas with the exterior. "In other words the crab when out of the water is able to breathe air" (1, p. 170). The invariable presence of an

air-chamber at the bottom of the burrow seems to support this view. It is probable in fact that the crab under its natural conditions practically is never out of the air. I kept several fiddlers in a jar the bottom of which was covered with a very thin layer of moist sand (2-3 mm.). The jar was covered and thus the atmosphere within it was saturated with vapor. The gill-chamber was prevented from drying but at the same time there was no chance of changing its liquid. Under such conditions the crabs lived very well for over 6 weeks and would probably have lived much longer had I not broken the experiment up. I failed to find anywhere data as to how long a fiddler may live under the water. Schwartz and Safir mention only that probably the fiddlers "do not find prolonged submergence very comfortable" (15, p. 19). And yet my fiddlers lived under the water for 6 weeks without showing any abnormalities and are still alive. To the end of this time they move rapidly when frightened and feed on mussels under the water. It is clearly to be seen that the flagella make their rhythmic movements, which in all crabs serve for renewing water in the gill-chamber. So the fiddler crabs seem to be true water-breathing forms like all other crabs. But at the same time the contents of their gill-chamber may be thoroughly ventilated in the air. It does not mean that they breathe air, nevertheless such a wide scale of adaptation furnishes an interesting example. The last experiment does not support the opinion of Abbott that the liquid of the gill-chambers has a lower osmotic pressure as compared with the sea water. It seems to me rather that this liquid cannot be anything else than the pure sea water.

3. A further question arises: why is the burrow of a fairly definite length, or, what conditions cause the crab to stop its working? There are several possibilities which may be tested experimentally.

The crab may stop after having expended a certain amount of energy in digging. But the resistance of the ground may be very different depending on the degree of moisture, presence of mud, small stones, plant roots, etc. The amount of spent energy may be very different in every single case and yet there is no evidence that the length of the burrow is affected by those

factors. They bear undoubtedly only on the time of digging. In some experiments I put a glass ring at the periphery of the jar covering it with a layer of sand about 3 cm. high. The crab digging close by the wall soon reached the obstacle and for several minutes it tried to remove it. It abandoned then the burrow and began to dig another one in the neighborhood which it abandoned in turn. The animal made 5 successive holes until it succeeded in bending the canal towards the middle of the jar and in avoiding the obstacle. The total amount of expended energy was certainly much greater than in the usual case and yet the animal dug its hole to the very bottom of the jar. The whole process lasted about 6 hours, during which *Uca* was constantly working, while an ordinary burrow is made easily in half an hour. In another series of experiments I mixed the sand with at least the same quantity of small stones (about 6 mm. in diameter). The resistance of the ground was very much increased, in fact about 3 times as measured roughly by determining the weight which was necessary for driving a nail into the sand and into the mixture. Nevertheless the crab succeeded in making a regular hole reaching to the bottom of the jar, which lasted however for about 20 hours. The amount of energy is different depending on the degree of inclination of the canal towards the horizon, as carrying the sand out from a steep burrow requires a greater strain. And again this does not bear on the length of the burrows.

Another possibility is that the crab may estimate the total length of the burrow while carrying the sand pellets out. But one observation speaks against the validity of this factor. The mode of burrowing described above is a type which does not mean however that it is to be observed the most frequently. In very many cases the crab works in a slightly different manner. When the burrow is just deep enough to hide the animal, *Uca* comes out of it, turns its big claw towards the burrow and enters again. The legs II., III. and IV. grasp the sand from the bottom, but the pellet is not carried out of the hole. The legs push it towards the opening, while the body remains at the same spot. The pellet comes to lie between the sternum of the crab and the wall of the canal. Still pushing it with the external

surface of the legs II., III., IV., the crab forces its own body below the pellet, grasping it with the legs 2, 3, 4. The sand is carried then to the mouth of the burrow and the legs 2, 3, 4, helped effectively by the small claw adjust the pellet at the edge of the hole. The second or the third pellet close the hole entirely, while the crab still continues the same work, grasping the sand at the bottom and adjusting it at the roof. As the work progresses the chamber containing the fiddler comes to lie still deeper under the surface and the sand-cork becomes still thicker. When the bottom of the jar is reached *Uca* spends a considerable time in working at the end-chamber and finally it quiets down, sometimes for many days. During the whole work the crab has no chance of measuring the length of the burrow as it is working itself through the sand. I think therefore that this factor may be also excluded.

If the importance of both mentioned factors is somewhat doubtful, it is sure that the degree of moisture plays a rôle in estimating the depth of the burrow. Even during the low tide I always found water at about one foot below the surface of the fiddler-ground. The burrow cannot go so far, for the walls of the end-chamber would collapse under the water. Testing the natural burrows with a long pipette I never found water there. The question may be solved experimentally. Usually I performed my experiments in the following way. I put sand into the jar and poured enough water to cover it completely. By stirring, droplets of air were removed. Then a long pipette was forced through the sand to the very bottom of the jar and the water was sucked out as far as possible. Under such conditions the crabs dug always to the bottom. But if we put the pipette only to half of the thickness of sand sucking water out, the animal will stop working when the level of water is reached. The degree of moisture influences then the depth of the burrow.

Unfortunately it is also sure that this factor is not the sole one. The natural burrows measured on an area of about one square meter on a perfectly flat ground may reach a very different level below the surface of the sand in spite of the exactly equal rising of the degree of moisture for all of them. Thus I am unable to answer exactly even such a simple question as why the burrow

is of a definite length. One is sure that the behavior of a *Uca* is determined by very many different factors.

4. The question of periodicity in the life of the fiddler crab is a very complicated one, as there are some theoretical objections. In my opinion the problem of intrinsic periodicity of the life phenomena resembles very much the famous problem of the inheritance of acquired characters. The rising tide brings a variety of factors with it and so does the falling tide. The life of a crab is fairly periodic and this is due to an approximative periodicity of external factors. Now if we observe the animal in the laboratory where conditions are fairly constant, there are no factors which in nature cause the rhythmicity of behavior. How could we expect such a rhythmicity? Every kind of activity is a reaction to certain stimuli. The peculiar character of all these reactions is hereditary and fairly constant for each species. But it surely does not mean that in the entire absence of those stimuli the reactions would remain the same. Such a "memory" is an obvious impossibility. If the causes are absent the effect will be absent also. We do not think that under natural conditions the periodicity of behavior of a fiddler is due entirely to the "memory" and not to the periodicity of tides. But only in this case we could expect the animal to behave rhythmically under the constant laboratory conditions. As to the cause of all rhythmicity, the tides, it is interesting to note that they are not rhythmic at all. I quote a random instance from Eldridge's Tide-Book for 1925. Successive intervals between the high-tide, low-tide, high-tide, etc., during the ten days are, in minutes:

349	308	389	316
406	380	360	426
341	356	324	364
401	399	419	376
346	312	385	311
410	430	360	431
353	381	321	349
389	371	419	390
344	321	379	308
412	421	365	434

The lowest interval is 308, the highest 434, which corresponds or a difference of 2 hours 6 minutes. As such an irregularity runs all the year round it would be a pure wonder if the "memory" would compel an animal living under constant conditions to accomplish its tasks at the same intervals. I do not intend to discuss the rich literature on periodicity of organic functions, but I have a strong impression that the whole question has a lot of metaphysics in it.

In fact I never noticed any intrinsic periodicity in my crabs. When put into the jar the crab digs the burrow, closes it and remains in the air-chamber for a very various time. Sometimes it will dig itself out in a few hours, sometimes it remains quiet for 3-4 days. If we put water into the jar while the chamber is tightly closed the crab does not go out even for a week. If we suck all water out *Uca* usually digs itself out in 3-4 hours, but sometimes it does not stir for many days. Its behavior must be ascribed to actual external factors, not to the remembered ones, although we are very far from understanding which factors are working. When the sand begins to dry *Uca* closes the burrow. It does the same when we pour slowly water into the jar and the sand becomes wet. From a certain point of view such reactions may be called memory, since the crab does the same as it has done under its natural conditions. We imitate those conditions as closely as possible and sometimes we get the same reaction. It is also not true that the fiddler closes its burrow "before the tide." It does it always *during the tide*, when the slowly rising water has moistened the air-chamber, not yet covering the surface of the ground. The arising slight movement of sand grains or the walls of the chamber becoming softer may be perceived by the crab as the beginning of the tide. As far as I observed *Uca* never remains a long time on the surface of the ground without visiting from time to time its burrow.

And thus, exactly as in heredity, not a given reaction in itself characterizes an animal, but always the faculty of producing this reaction *under given conditions*.

5. What becomes of the burrow after the tide? The tide destroys a part of the burrow and the crab must dig itself out. This may be done in several manners and I must confess that

the interpretation is very difficult. As mentioned above a quick pouring of water in the jar causes the walls to collapse, thus destroying the burrow completely. The animal forces itself through the sand and after the water has been removed it digs a new burrow in quite a new spot. But if the burrow was tightly closed *Uca* begins to work methodically, provided that the "tide" has gone out. Its movements are now somewhat the reverse of the ordinary burrowing. It will be remembered that the animal while remaining motionless in the air-chamber has its large chela directed to the inside. Now the outer legs, 2, 3, 4, grasp a sand pellet from the roof of the chamber and push it down towards the sagittal axis of the body. Then the crab climbs a little upward until the pellet lies between the carapace and the legs II., III., IV., which grasp it in turn. *Uca* comes down again and the sand will be deposited and kneaded at the bottom of the chamber. Still pursuing this work, the animal causes the chamber to rise slowly in an oblique direction, still keeping its volume unaltered, as the sand is always only carried from the roof of it to the bottom. At last the fiddler emerges, leaving the former canal filled with sand behind itself. Only the upper part of the burrow corresponding to the chamber in the last moment of work remains open. Now the crab may roam for a long time around the jar or it will start digging a new burrow at once. In most cases it works now along the same way, entering the hole from which it has emerged and following the same track. Usually it carries then the removed sand out of the burrow and the whole canal remains open. But, curiously enough, often will the crab close the canal behind it. After some time *Uca* is sitting again in the air-chamber at the bottom of the jar, while the whole burrow is tightly filled with sand, as if the animal wanted only to breathe fresh air for a while. In following the previous track the crab is evidently guided by the smaller resistance of the sand filling the burrow as compared with the surrounding. If the jar was filled with water for some time the sand collapses and there is no difference in its consistency. In this case *Uca* digs itself out once more, but does not follow exactly the previous track and sometimes it will dig in a perfectly vertical direction. In the apparatus

described above, where the fiddler had to dig between two glass plates, this exact following of the former track may be easily observed. A female dug a vertical hole (Fig. 3, *a*) and then the whole apparatus was turned at right angles. The crab changed the direction of the digging (Fig. 3, *b*). All the time the burrow remained filled with sand save the end-chamber. On the following morning I found the female out of the apparatus and the hole showed conditions as on Fig. 3, *c*. The track of digging could be distinctly followed and it corresponds exactly to the previous one.

Nevertheless such a behavior is not a rule and I have seen many times that the crab may choose an entirely new direction. One individual has dug itself out and the burrow remained open for several hours. Then it entered into it, grasped sand from the bottom and carried it to the opening, closing it in the usual way. *Uca* then proceeded to work until the whole canal became tightly filled with sand. During the work the end-chamber increased both in volume and length, directing itself obliquely upward but at right angles to the former burrow. After having closed the burrow the crab immediately started again the work of digging itself out in the new direction. It detached pellets from the roof and deposited them at the inner corner of the chamber. After some time a new open burrow was manufactured and as the end-chamber has increased considerably during the previous work it had now room enough for all sand detached from its roof. As a result there was a new open burrow at right angles to the first. I am unable to say what may be the biological significance of such a peculiar behavior.

We see clearly at least that closing the burrow before high tide and opening it at low tide by no means covers the whole field of the behavior of a fiddler crab. It is merely a scheme under which lies a whole world of varied, complicated and as yet perfectly incomprehensible activities.

6. The most difficult problem, of course, is the problem of interpretation. I do not know how to characterize the behavior of *Uca*. Is it reflex, instinct, or intellect? It will be probably safer to speak about the "activities" and it is certainly more important to investigate which are the real properties of those

activities than to reason about what they are and how to call them.

There is one striking property of very many reactions which I would like to insist upon: their plasticity. In fact, the closer we watch a fiddler the more obvious becomes the conclusion that there is very little automatic in it. The practical mode of accomplishing the various tasks depends on an infinity of minute circumstances which are so various and different that surely never two crabs work at their burrows under exactly the same conditions. The animal performs its tasks *in spite of* the condition being so various, and yet there is no doubt that every single movement is largely depending on external stimuli. When the pellet is carried out, the sand must be prevented from falling back into the hole. And we see that in every single case the sand is pushed, pulled and kneaded *until* it becomes properly adjusted. Yet the properties of a pellet, as its size, its form, the degree of moisture, the contents of organic matter and of clay, the position towards the walls of the burrow, towards the mouth of it, towards the other pellets, etc., are never the same. All those properties bear very strongly on the actual movements of the animal, which has to adjust not simply "a pellet of sand" but always *this single pellet* with all its individual particularities. The crab is always so careful about it that only rarely a few grains roll back into the hole and it must estimate and judge whether the work is done sufficiently well. Every single activity connected with burrowing may be analyzed in the same way. Choosing the spot where the burrow is to be made, grasping the sand, carrying the pellet out, turning in the burrow so as to make it circular, taking care of the burrow being conveniently bent, conveniently oblique, of a definite length, avoiding the obstacles, manufacturing the chamber, closing the burrow in various manners, adapting the mode of acting to a situation which is different in every successive second, each of those activities again may be performed in infinitely different ways. But they all bear on burrowing, which is only a small part of the whole behavior of a fiddler crab.

Given this unlimited variety of reactions, it becomes utterly impossible to admit that each single reaction is referable to a

particular fixed and unchangeable nervous mechanism. As may be deduced from the facts contained in the classical work of Bethe on the nervous system of *Carcinus*, this system is far too simple to be able to contain such a variety of reflex arcs. It does not follow from this that the activities may be controlled by something besides the nervous system. But it certainly follows from this that the morphology is of little help to us. We are compelled to admit a plasticity of the nervous centers; they must possess a certain creative power which enables them to become adapted to entirely new situations. The number of possible nervous connections is limited, but the number of possible reactions is infinite. This discrepancy may be avoided only by admitting that each nervous center may perform an infinity of functions.

SUMMARY.

The typical mode of digging a burrow is described and some problems discussed which are closely connected with the burrowing instinct.

The choice of the spot where the digging is started is determined by very many factors. Phototaxis and thigmotaxis are not sufficient explanations.

The end-chamber of the burrow functions as an air-chamber during the high tide.

The fiddler crab is a true water-breathing animal, but it can live in the air for several weeks without changing the water in the gill-chambers.

The length of the burrow partly depends on the degree of moisture of the ground.

There is no intrinsic periodicity in the life of *Uca*.

Several modes of closing the burrow and opening it are described.

In the interpretation the plasticity of activities is strongly insisted upon.

WOODS HOLE,

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LITERATURE.

1. Abbott, J. F.

'12-'13 The Effect of Distilled Water upon the Fiddler Crab. BIOL. BULL., Vol. 24.

2. Alcock, A.

'92 On the Habits of *Gelasimus annulipes* Edw. Ann. Mag. Nat. Hist., Vol. VI.

3. Bethe, A.

'97-'98 Das Nervensystem von *Carcinus Maenas*. Arch. f. mikr. Anat., Bd. 50, 1897, pp. 460 and 589. Ibid., Bd. 51, 1898, p. 382.

4. Clark, G. P.

'95-'96 On the Relation of the Otocysts to Equilibrium Phenomena in *Gelasimus pugilator* and *Platyonichus ocellatus*. The Journ. of Physiol., Vol. XI X.

5. Cowles, R. P.

'08 Habits, Reactions, and Associations in *Ocypoda arenaria*. Papers from the Tortugas Lab. Carnegie Inst. Wash., II.

6. Dembowski, J.

'23 Über die Bewegungen von *Paramæcium caudatum*. Arch. f. Protistenkde, Bd. 47.

7. Dembowski, J.

'23 Experimental biologische Studien über die Larve der Köcherfliege *Molanna*. Travaux de l'Inst. M. Nencki Varsovie., Vol. II. (Polish).

8. Dembowski, J.

'25 Experimentelle Untersuchungen über das Verhalten der Krabbe *Dromia vulgaris*. Teil I.-III. Ibid., Vol. III. (Polish).

9. Frisch, K. v.

'23 Über die "Sprache" der Bienen. Zoolog. Jahrb. Allg. Zool., Bd. 40.

10. Garner, R. L.

'92 The Speech of Monkeys. New York.

11. Holmes, S. J.

'08 Phototaxis in the Fiddler Crab and Its Relation to the Theories of Orientation. Journ. Comp. Neur. Psych., Vol. 18.

12. Hyman, O. W.

'20 Adventures in the Life of a Fiddler Crab. Ann. Rep. Smithson. Inst.

13. Kingsley, S. y.

'88 Something About Crabs. Amer. Nat., Vol. 22.

14. Pearse, A. S.

'13 Habits of Fiddler Crabs. Ann. Rep. Smiths. Inst.

15. Pearse, A. S.

'14 On the Habits of *Uca pugnax* (Smith) and *Uca pugilator* (Bosc). Trans. of the Wisconsin Acad. Sc. Arts. Lett., Vol. XVII.

16. Rathburn, M. J.

'18 The Grapsoid Crabs of America. U. S. Nat. Mus. Bull. 97.

17. Schwartz, B., and Safir, S. R.

'15 Habit Formation in the Fiddler Crab. Journ. of Anim. Behavior, Vol. 5.

18. Schwartz, B., and Safir, S. R.

'15 The Natural History and Behavior of the Fiddler Crab. Cold Spring Harbor Monographs, VIII.

19. Symons, C. T.

'21 Notes on Certain Shore Crabs. Spolia Zeylanica, Colombo, XI.

20. Wasmann, E.

'09 Die psychischen Fähigkeiten der Ameisen. 2 Aufl. Stuttgart.